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Field screening maize germplasm for resistance and tolerance to western corn rootworms (Col.: Chrysomelidae)†

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Abstract: In the hopes of lessening the current reliance on soil insecticides, developing a viable alternative for transgenic maize hybrids, and providing sustainable options for Europe, researchers recently have been developing novel maize lines that exhibit resistance and/or tolerance to corn rootworm larvae. Here we report the results of a 2-year field experiment in a northern growing region assessing the resistance and tolerance of 10 experimental synthetic maize populations selected for varying levels of damage from western corn rootworm larvae, *Diabrotica virgifera virgifera* LeConte (Col.: Chrysomelidae) and four maize hybrids. Maize non-preference, antibiosis and tolerance to rootworms was evaluated using previously established methods, including: the Iowa 1–6 root damage rating scale, root fresh weight, compensatory root growth ratings and adult rootworm emergence. Among the experimental synthetic maize populations, BS29-11-01 was the most susceptible, and had a mean root damage rating that was greater than the highly susceptible maize hybrid B37 × H84. This line also had the lowest mean root fresh weight and one of the lowest mean compensatory root growth ratings. In contrast, CRW8-3 appeared to be tolerant to western corn rootworms, and had the lowest mean root damage rating, which was comparable with that of the non-transgenic hybrid DeKalb® 46-26.

Key words: *Diabrotica v. virgifera*, maize breeding, plant resistance, root pests

1 Introduction

Corn rootworms (Chrysomelidae: *Diabrotica*) are insect pests that can cause economic damage to maize (*Zea mays* L.) by consuming root tissue, thus negatively impacting plant physiology and function (Riedell 1990; Hou et al. 1997; Riedell and Reese 1999), and increasing the likelihood of plant lodging (Sutter et al. 1990). The end result is a reduction of yield (Sutter et al. 1990; Spike and Tollefson 1991), which means less money for producers. In 1986, corn rootworms and their management cost farmers approximately 1 billion dollars per year (Metcalf 1986), although this statistic is likely to have changed. Soil insecticides and crop rotation are commonly used to manage rootworm pests (Wilson et al. 2005) with almost 2 million kg of rootworm-registered insecticides applied in the United States in 2005 (USDA 2006). Crop rotation has been an effective control method; however, the rootworms have adapted to this strategy in some areas by laying eggs in alternate crops such as soybean (*Glycine max* L.) (Levine et al. 1992), or extending their diapause from 1 to 2 years (Krysan et al. 1984; Levine et al. 1992).

Because of negative aspects of broad-spectrum pesticide use, the decline of the effectiveness of crop rotation in many areas, and the establishment of the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, in Europe, there is an increasing need for alternate rootworm management strategies, including using resistant and/or tolerant maize hybrids. The US Environmental Protection Agency has registered transgenic hybrids that express insecticidal proteins derived from *Bacillus thuringiensis* Berliner (Bt) targeting corn rootworms; however, these pests have already developed resistance to some insecticides (Ball and Weekman 1962; Meinke et al. 1998). Models predict that pests could eventually develop resistance to transgenic corn (Crowder and Onstad 2005), which would dramatically affect our ability to manage these pests, although many factors can impact the evolution of resistance (Mitchell and Onstad 2005; Sisterson et al. 2005).

†Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the US Department of Agriculture.

Scientists have been trying to identify maize lines with rootworm resistance in the hopes of lessening reliance on insecticides and developing viable alternatives to transgenic corn hybrids (Branson et al. 1983; Gray and Steffey 1998; Hibbard et al. 1999). Investigations have focused on screening germplasm of maize and its relatives for use in breeding programmes (Branson 1971; Moellenbeck et al. 1995; Hibbard et al. 1999; Eubanks 2002), refining evaluation methods regarding plant susceptibility (Moellenbeck et al. 1994; Knutson et al. 1999), and exploring mechanisms of resistance (Ajani and Lonnquist 1979; Xie et al. 1992; Assabgui et al. 1995). There has been an active germplasm screening programme in the southern Corn Belt for over a decade (Hibbard et al. 1999). Several maize lines have exhibited some resistance to corn rootworms in this location (Hibbard et al. 1999). However, because environmental factors, such as soil type and temperature, can affect maize physiology and rootworm behaviour (Turpin et al. 1972; Dominique et al. 1983; Jackson and Elliott 1988; Woodson et al. 1996), it is important to evaluate experimental germplasm in multiple geographic locations.

There are three mechanisms of plant resistance: (i) non-preference (or antixenosis); (ii) antibiosis and (iii) tolerance (Painter 1951). Non-preferred plants are not eaten or used for oviposition as frequently as preferred ones, while plants exhibiting antibiosis have negative effects on pest life history parameters or performance (Painter 1951). The impact of non-preference vs. antibiosis on rootworms can be difficult to distinguish, and are often collectively referred to as resistance (Grabstein and Scriber 1982; Blossey and Hunt-Joshi 2003). Historically, root damage ratings and adult emergence have been used to measure both traits (Branson et al. 1983; Branson 1986). Tolerance is the plant's ability to cope with and respond to herbivore damage (Painter 1951), and is related to root size and compensatory root growth ratings (Branson 1986; Riedell and Evenson 1993; Blossey and Hunt-Joshi 2003). However, root growth that occurs in response to rootworm damage can negatively impact maize yield, especially when adequate moisture is present (Gray and Steffey 1998).

Our objectives were to evaluate the resistance and tolerance of 10 experimental synthetic maize populations and four maize hybrids to western corn rootworm in a northern growing region which had previously been selected for varying levels of resistance from a southern growing region. We assessed the performance of a transgenic resistant hybrid (DeKalb® 46-23, Monsanto, St. Louis, MO), and commercial hybrids currently available to farmers (DeKalb® 46-26, B73 × MO17, B37 × H84) to determine how maize lines used in breeding programmes measure up to elite hybrids in the same environment. We used previously established methods (Chiang 1973; Branson 1986; Mayo 1986) to assess plant resistance and tolerance, including: the Iowa 1–6 root damage rating scale (Hills and Peters 1971), root fresh weight, compensatory root growth ratings, and density and weight of emerging adult rootworms.

2 Materials and Methods

2.1 Experimental plot setup

The experiment was conducted in 2005 and 2006 at the Eastern South Dakota Soil and Water Research Farm near Brookings, SD (United States Department of Agriculture, Agricultural Research Service and Northern Plains Area). Maize lines were planted in a field previously managed under a 4-year rotation of maize, soybeans, oats and spring wheat to ensure that experimental plots were not contaminated by surrounding natural rootworm populations.

To determine appropriate fertilization levels, the soil was sampled on 4 April 2005 and 12 April 2006 from five locations throughout the field and sent to a soil testing lab (South Dakota State University, Soil Testing Lab, Brookings, SD). In 2005, 157 kg/ha starter fertilizer (14-36-13) and 151 kg/ha urea (46-0-0) were surface applied, while in 2006, 177 kg/ha starter (14-36-13) and 105 kg/ha urea (46-0-0) were applied. Fertilizer was applied to the field (19 × 20 m) with a plot fertilizer spreader (10′ model, Barber Engineering Co., Spokane, WA) and incorporated into the top 10 cm of soil via field cultivation.

There were 14 one-row plots per replicate with one maize genotype per plot. The treatments included 10 experimental synthetic maize populations with a range of rootworm resistance levels [NGSDCRW1(S2)C4, CRW8-1, CRW8-2, CRW8-3, CRW2(C5), CRW3(C6), SD10, BS29-18-01, BS29-07-01 and BS29-11-01; table 1], a transgenic resistant hybrid expressing the Cry3Bb1 endotoxin with rootworm resistance (DeKalb® 46-23), its non-transgenic isoline (DeKalb® 46-26), and two susceptible public hybrids (B73 × MO17 and B37 × H84). DeKalb® 46-23 and DeKalb® 46-26 seeds were pre-treated with two fungicides (metalaxyl and mefenoxam) and the insecticide clothianidin, while seeds from the other hybrids and experimental lines were not treated.

We utilized a randomized complete block design with four replications. On 16 May 2005, buffer rows (DeKalb® 440) were sown at the recommended density of 74,130 seeds/ha using an eight row vacuum planter (Max Merge 7200, John Deere, Moline, IL), while on 12 May 2006 buffer rows (DeKalb® 46-26) were sown at the recommended density of 63,010 seeds/ha. Experimental rows had 1.3 m of buffer plants on each end which were hand planted using jab planters, row spacing was 0.76 m, and plots were 3.43 × 0.76 m.

Seeds were hand planted on 19 May 2005 and 16 May 2006 using jab planters (Easy-Plant Model 98; R. T. Adkins, Parsonsburg, MD). In 2005, there were 10 seeds per one-row plot, with one buffer plant followed by five plants for evaluating root damage, three plants used for determining compensatory root growth, and a final buffer plant. Because we monitored adult emergence in 2006, there were 15 seeds per one-row plot, with one buffer plant, then four plants for measuring root damage, another buffer plant, three plants for evaluating compensatory root growth, an additional buffer plant, four plants used to monitor emergence and a final buffer plant. Seeds were planted 5.0 cm deep and had 23.0 cm within-row spacing, which is equivalent to 57,400 seeds/ha. There were no formal buffer plants between experimental plots; however, the first and last plant in each experimental plot were not sampled.

On 19 May 2005, plots were sprayed with the pre-emergent herbicide Dual® II Magnum® (2.3 l/ha; Syngenta, Greensboro, NC), while on 5 May 2006 plots were sprayed with Dual® II Magnum® (2.3 l/ha) and

Table 1. *Background information on maize hybrids and experimental synthetic maize populations grown in field trials near Brookings, SD during 2005 and 2006*

Pedigree		Background	Source	References
NGSDCRW1 (S2)C4	SP	Moderate resistance in MO	NCRPI, USDA-ARS, SDSU AES	Kahler et al. 1985, Hibbard et al. 1999
CRW8-1	SP	High resistance in MO, derived from BS19/20	USDA-ARS, Columbia, MO	Russell et al. 1976
CRW8-2	SP	High resistance in MO, derived from BS19/20	USDA-ARS, Columbia, MO	Russell et al. 1976
CRW8-3	SP	High resistance in MO, derived from BS19/20	USDA-ARS, Columbia, MO	Russell et al. 1976
CRW2(C5)	SP	High resistance, derived from CIMMYT in Hibbard et al. 1999	USDA-ARS, Columbia, MO	Russell et al. 1976, Hibbard et al. 1999
CRW3(C6)	SP	High resistance, derived from Hibbard et al. 1999	USDA-ARS, Columbia, MO	Russell et al. 1976, Hibbard et al. 2007
BS29-18-01	SP	Susceptible in MO, derivative of BS29	Iowa State University	Hallauer 1994, GRIN NPGS 2006, B. E. H
BS29-07-01	SP	Susceptible in MO, derivative of BS29	Iowa State University	Hallauer 1994, GRIN NPGS 2006, B. E. H
BS29-11-01	SP	Susceptible in MO, derivative of BS29	Iowa State University	Hallauer 1994, GRIN NPGS 2006, B. E. H
SD10	SP	Moderate resistance in MO, tolerant to rootworms	SDSU	Chiang 1973, B. E. H
DeKalb® 46-23 CRW	H	Transgenic resistant hybrid	Monsanto	
DeKalb® 46-26	H	Non-transgenic isoline of DeKalb® 46-23	Monsanto	Monsanto Company 2006
B73 × MO17	H	Susceptible hybrid, some tolerance	Public line	GRIN NPGS 2006, B. E. H
B37 × H84	H	Highly susceptible hybrid	Public line	GRIN NPGS 2006

Resistance/suceptiblity assessed in MO trials using root damage ratings.
B. E. H, Bruce E. Hibbard (personal communication); GRIN NPGS, Germplasm Resources Information Network, National Plant Germplasm System; H, maize hybrid; MO, Missouri; NCRPI, North Central Regional Plant Introduction Station; SDSU AES, South Dakota State University, Agricultural Experiment Station; SP, experimental synthetic maize population; USDA-ARS, United States Department of Agriculture, Agricultural Research Service.

Roundup® (2.3 l/ha, Monsanto) for grass control. On 15 June 2005 and 5 June 2006 plots were sprayed with the post-emergent herbicide Callisto® (0.2 l/ha, Syngenta) for broadleaf weed control.

Experimental rows in field plots were mechanically infested on 17 May 2005 and 15 May 2006 with 1000 viable western corn rootworm eggs per 30 cm suspended in a 0.15% agar solution (Palmer et al. 1977) using Sutter and Branson's (1980) technique. Buffer rows were not infested with rootworm eggs, which were obtained from the primary diapausing colony maintained at the North Central Agricultural Research Laboratory in Brookings, SD. Hatch controls were performed prior to infestation to determine the percentage of hatched eggs. Using a fine paintbrush, three batches of 100 eggs were placed on moistened filter paper in separate Petri dishes (100 × 15 mm), incubated at 25°C, and monitored for up to 4 weeks. In 2005, 87 ± 2% of the eggs hatched, while in 2006, 86 ± 4% of the eggs hatched. Plants were infested with eggs at a depth of 8–10 cm, and experimental rows were infested 0.3–0.6 m beyond plot boundaries.

To estimate western corn rootworm development and maximum root feeding damage, on 18 May 2005 and 16 May 2006 we placed the soil probe of a biophenometer (Model: BIO-51-TP03C; Omnidata® datapod, Logan, UT) 8.9–10.2 cm into the soil and monitored growing degree days with an upper threshold of 35°C and a lower threshold of 11°C (Fisher et al. 1990). We used soil growing degree days to determine timing of root evaluation instead of monitoring adult emergence, because plants could not grow normally if covered by emergence cages.

2.2 Root damage, root weight and compensatory root growth

On 11 July 2005 and 12 July 2006, five (2005) or four (2006) consecutive roots per one-row plot were sampled and rated for root damage. Roots were dug after approximately 600 growing degree days to assess roots at maximum rootworm damage. Plant tops were cut above the lowest visible node and discarded, remaining stems labelled with waterproof tags, and roots dug with a four pronged potato fork. Loose soil was removed by tapping and roots soaked outside in mesh baskets suspended in tanks of water with water softener (1.9 l/tank; Calgon®, Reckitt Benckiser Inc., Wayne, NJ) to help loosen soil balls. After 24–48 h, roots were washed with high pressure sprayers (400 maximum pound per square inch) to remove remaining soil. Roots were then placed within doubled plastic garbage bags and stored in a 7.2°C cold room to retain moisture and prevent deterioration.

After 4–8 days, roots were cut at the seventh node and fresh weight recorded. They were then rated for rootworm damage using the Iowa 1–6 scale (Hills and Peters 1971). This rating scale uses the following criteria: 1, no root damage or a few feeding scars; 2, feeding scars, but no roots pruned to 3.8 cm (1.5 inch) of the plant; 3, several roots pruned to 3.81 cm, but an entire node of roots not pruned; 4, one node of roots pruned; 5, two nodes pruned and 6, three or more nodes pruned.

On 16 September 2005 and 9 August 2006, three consecutive roots per one-row plot were dug to assess compensatory root growth. Roots were treated in the same manner as above. After 1–9 days, roots were rated relative to one another using the following scale (1, least compensatory root growth; 5, most compensatory root growth; modified from Owens et al. 1974).

2.3 Rootworm emergence

To monitor the density of adult rootworms originating from each experimental plot, emergence cages were installed on 10 July 2006 for all maize lines, except SD10 because of poor germination and a lack of plants. Four consecutive maize plants were cut at soil level, and weeds and detritus removed. Cages (61 × 102 cm) were set into shallow trenches (8 cm), which were then filled with soil to seal the cage bottom. Cages had 26 gauge galvanized sheet metal sides and a mesh screen top, and were tapered to guide beetles upwards to the plastic collection tube (Chaddha et al. 1993). Beetles entered the collection tube through an inverted mesh cone, which prevented them from exiting. Insecticide-impregnated plastic (1.3 × 1.3 cm; PROZAP® Insect Guard™, Chem-Tech Ltd., Des Moines, IA) was placed in collection tubes to kill emerging adults. Rootworm adults were collected from cages on: 14 July, 19 July, 24 July, 28 July, 2 August, 7 August, 11 August, 18 August and 23 August 2006. Adults were placed into labelled plastic cups and frozen at −20°C. Rootworms were sexed and counted using a dissecting microscope (65-100X; Wild M3Z, Heerbrugg, Switzerland), then dried in a 60°C oven (Thelco Precision oven, model 6547; Thermo Electro Corp., Marietta, OH) for 21 h and weighed (Explorer® Pro, model EP214C; Ohaus®, Pine Brook, NJ).

2.5 Statistics

Because modern elite hybrids have been bred for superior performance, including high levels of vigour that may contribute to rootworm resistance and/or reduced root damage, comparing them to experimental populations may not be equitable, so we analysed each group (experimental synthetic maize populations and hybrids) separately. Additionally, measurements of plant resistance or tolerance to rootworms from each year were combined for analysis (2005 + 2006 data), because the mean across both years is likely a more accurate indicator of maize line performance.

The GLIMMIX procedure in (SAS® 2004, 2005) followed by Tukey's Honest Significant Difference (HSD) test were used to analyse root damage ratings, root fresh weight and compensatory root growth ratings. Root damage ratings, root fresh weight or compensatory root growth ratings were the response variables, while maize line was the independent variable.

Rootworm emergence data were $\log(X + 1)$ transformed and analysed using repeated measures ANOVA in SYSTAT® (SPSS Inc. 1998) with sample date as the dependent variable, maize line as the independent variable and log of mean fresh root weight from 2006 as the covariate. If time × line interactions were not significant, data were analysed with ANOVA and Tukey's HSD *post hoc* tests, with rootworm data (number of males, male weight, number of females or female weight) as the dependent variable, maize line as the independent variable and log of mean fresh root weight from 2006 as the covariate. Covariate analysis was used because resource availability (i.e. amount of root tissue) could potentially impact rootworm emergence and beetle weight. Correlations between rootworm density and weight were calculated using least squares linear regression in SYSTAT® (SPSS Inc. 1998).

3 Results

Data from maize line SD10 were not used because this line had extremely poor germination and growth, which likely produced invalid results.

3.1 Root damage ratings

Maize line significantly affected root damage ratings within experimental synthetic maize populations (d.f.$_{8,309}$, $P < 0.001$; table 3). BS29-11-01 had significantly more root damage than all of the other synthetic maize populations ($P < 0.05$), with the exception of BS29-07-01 ($P = 0.92$; table 2). Additionally, CRW8-1, CRW8-3 and CRW3(C6) had significantly less root damage than BS29-07-01 ($P = 0.005$, $P < 0.001$ and $P = 0.007$; table 2). For some synthetic maize populations, root damage ratings were variable from 2005 to 2006 (table 2).

Maize line also significantly influenced root damage ratings of maize hybrids (d.f.$_{3,137}$, $P < 0.001$).The transgenic hybrid DeKalb® 46-23 had significantly lower root damage than its isoline DeKalb® 46-26 ($P < 0.001$), the susceptible hybrid B73 × MO17 ($P < 0.001$) and the highly susceptible hybrid B37 × H84 ($P < 0.001$; table 3). In addition, DeKalb® 46-26 and B73 × MO17 had significantly lower root damage than B37 × H84 ($P < 0.001$, $P = 0.02$; table 3). Mean root damage ratings of maize hybrids were fairly consistent from 2005 to 2006, with the exception of B37 × H84, which had higher root damage in 2006 (table 3).

3.2 Root weight

Maize line had a significant impact on root fresh weight of experimental synthetic maize populations (d.f.$_{8,309}$, $P < 0.001$). NGSDCRW1(S2)C4 roots were significantly heavier than roots of all other synthetic maize populations ($P < 0.05$; table 2). Additionally, CRW8-2 and CRW8-3 roots were significantly heavier than BS29-07-01 ($P = 0.02$, $P = 0.002$) and BS29-11-01 ($P = 0.004$, $P < 0.001$; table 2). CRW8-1 roots weighed more than those of BS29-11-01, although the P-value was marginal ($P = 0.06$), while CRW3(C6) roots were significantly heavier than BS29-11-01 roots ($P = 0.03$; table 2).

Maize line also significantly influenced maize hybrid root fresh weight (d.f.$_{3,137}$, $P < 0.001$). The highly susceptible hybrid, B37 × H84, had significantly lower root fresh weight compared with the transgenic hybrid DeKalb® 46-23 ($P < 0.001$), DeKalb® 46-26 ($P < 0.001$), and the susceptible hybrid B73 × MO17 ($P < 0.001$; table 3). All of the maize hybrids had higher mean root fresh weights in 2006 (table 3).

3.3 Compensatory root growth ratings

Maize line had a significant effect on compensatory root growth ratings of experimental synthetic maize populations (d.f.$_{8,142}$, $P < 0.001$). CRW8-2 and CRW8-3 had significantly higher compensatory root

Table 2. *Mean root damage ratings, root fresh weight (g), and compensatory root growth ratings for nine experimental synthetic maize populations grown in field trials near Brookings, SD during 2005 and 2006*

Maize line	RDR[1] 2005	RDR[1] 2006	RDR[1] 2005–2006	Fresh weight[2] 2005	Fresh weight[2] 2006	Fresh weight[2] 2005–2006	CRGR[3] 2005	CRGR[3] 2006	CRGR[3] 2005–2006
NGSDCRW1 (S2)C4	2.5 ± 0.2	3.0 ± 0.3	2.7 ± 0.2 ab	87.6 ± 7.8	155.2 ± 8.4	116.6 ± 8.1 a	2.8 ± 0.4	4.4 ± 0.3	3.6 ± 0.3 ab
CRW8-1	2.7 ± 0.2	2.3 ± 0.1	2.5 ± 0.1 a	46.5 ± 3.9	102.9 ± 9.5	71.6 ± 6.6 bcd	2.4 ± 0.5	4.6 ± 0.2	3.6 ± 0.4 ab
CRW8-2	2.7 ± 0.1	3.0 ± 0.2	2.8 ± 0.1 ab	59.1 ± 6.0	102.6 ± 10.5	78.5 ± 6.7 b	3.6 ± 0.7	4.7 ± 0.2	4.3 ± 0.3 b
CRW8-3	2.2 ± 0.2	2.6 ± 0.2	2.3 ± 0.1 a	75.7 ± 7.7	94.9 ± 8.0	84.2 ± 5.7 b	4.3 ± 0.4	4.6 ± 0.2	4.5 ± 0.2 b
CRW2 (C5)	2.3 ± 0.2	3.5 ± 0.3	2.8 ± 0.2 ab	54.3 ± 6.7	88.8 ± 9.2	69.6 ± 6.2 bcd	2.6 ± 0.3	3.6 ± 0.4	3.1 ± 0.3 a
CRW3 (C6)	2.0 ± 0.2	3.2 ± 0.3	2.5 ± 0.2 a	66.2 ± 5.0	82.5 ± 11.2	73.5 ± 5.8 bc	2.8 ± 0.4	3.1 ± 0.2	3.0 ± 0.2 a
BS29-18-01	3.0 ± 0.3	2.8 ± 0.3	2.9 ± 0.2 ab	37.2 ± 4.1	97.2 ± 7.8	64.6 ± 6.6 bcd	3.4 ± 0.3	3.4 ± 0.4	3.4 ± 0.3 ab
BS29-07-01	4.0 ± 0.3	2.8 ± 0.1	3.4 ± 0.2 bc	27.1 ± 3.0	77.3 ± 6.9	49.4 ± 5.4 cd	3.0 ± 0.5	4.3 ± 0.2	3.8 ± 0.3 ab
BS29-11-01	3.2 ± 0.3	4.4 ± 0.2	3.7 ± 0.2 c	36.1 ± 2.9	55.3 ± 3.9	44.9 ± 2.9 d	2.3 ± 0.3	3.3 ± 0.3	3.0 ± 0.2 a

Statistics only done on multiyear data. Within each column means ± SEM followed by the same letter are not significantly different ($P > 0.05$).
[1]RDR, root damage ratings using the Iowa 1–6 scale (1, no root damage or a few feeding scars; 2, feeding scars, but no roots pruned to 3.8 cm of the plant; 3, several roots pruned to 3.8 cm, but an entire node of roots not pruned; 4, one node of roots pruned; 5, two nodes pruned and 6, three or more nodes pruned; Hills and Peters 1971).
[2]Fresh roots were cut at the seventh node and weighed.
[3]CRGR, compensatory root growth ratings (1, least growth; 5, most growth; based on Owens et al. 1974).

Table 3. *Mean root damage ratings, root fresh weight (g), and compensatory root growth ratings for four maize hybrids grown in field trials near Brookings, SD during 2005 and 2006*

Maize line[1]	RDR[2] 2005	RDR[2] 2006	RDR[2] 2005–2006	Fresh weight[3] 2005	Fresh weight[3] 2006	Fresh weight[3] 2005–2006	CRGR[4] 2005	CRGR[4] 2006	CRGR[4] 2005–2006
DeKalb® 46-23 CRW	1.0 ± 0	1.0 ± 0	1.0 ± 0 a	80.2 ± 3.7	104.1 ± 10.4	90.4 ± 5.3 a	1.0 ± 0	1.0 ± 0	1.0 ± 0 a
DeKalb® 46-26	2.2 ± 0.2	2.4 ± 0.2	2.3 ± 0.2 b	68.2 ± 4.6	106.0 ± 9.7	85.0 ± 5.9 a	1.5 ± 0.2	2.8 ± 0.3	2.3 ± 0.2 b
B73 × MO17	2.9 ± 0.2	2.3 ± 0.1	2.6 ± 1.5 b	57.8 ± 5.1	119.2 ± 5.8	85.1 ± 6.4 a	4.7 ± 0.3	4.6 ± 0.2	4.6 ± 0.2 c
B37 × H84	2.7 ± 0.2	3.8 ± 0.3	3.2 ± 0.2 c	35.1 ± 3.6	60.1 ± 4.9	46.2 ± 3.6 b	2.3 ± 0.3	2.2 ± 0.2	2.2 ± 0.2 b

Statistics only done on multiyear data. Within each column means ± SEM followed by the same letter are not significantly different ($P > 0.05$).
[1]DeKalb® 46-23 CRW is a transgenic resistant hybrid, DeKalb® 46-26 is the isoline of DeKalb® 46-23 CRW, B73 × MO17 is susceptible and B37 × H84 is highly susceptible.
[2]RDR, root damage ratings using the Iowa 1–6 scale (1, no root damage or a few feeding scars; 2, feeding scars, but no roots pruned to 3.8 cm of the plant; 3, several roots pruned to 3.8 cm, but an entire node of roots not pruned; 4, one node of roots pruned; 5, two nodes pruned and 6, three or more nodes pruned; Hills and Peters 1971).
[3]Fresh roots were cut at the seventh node and weighed.
[4]CRGR, compensatory root growth ratings (1, least growth; 5, most growth; based on Owens et al. 1974).

growth ratings than CRW2(C5) (P = 0.04, P = 0.007), CRW3(C6) (P = 0.006, P < 0.001), and BS29-11-01 (P = 0.02, P = 0.002; table 2). Additionally, mean compensatory root growth ratings for CRW8-3 were higher than those of BS29-18-01, although the difference was marginally statistically significant (P = 0.06; table 2).

Maize line also had a significant effect on compensatory root growth ratings of maize hybrids ($d.f._{3,63}$, P < 0.001). The transgenic hybrid DeKalb® 46-23 had significantly lower compensatory root growth ratings compared with its isoline DeKalb® 46-26 (P < 0.001), the susceptible hybrid B73 × MO17 (P < 0.001), and the highly susceptible hybrid B37 × H84 (P < 0.001; table 3). Furthermore, B73 × MO17 had significantly higher compensatory root growth ratings compared with DeKalb® 46-26 (P < 0.001) and B37 × H84 (P < 0.001; table 3).

3.4 Emergence

For experimental synthetic maize populations, emergence data (number of adult males and male weight) from 2, 16 and 23 August were excluded from repeated measures analysis because all values were zeros, while for maize hybrids data from 28 July to 23 August were excluded. Over the dates used for analysis, male emergence and male weight was relatively constant for maize hybrids, whereas for synthetic maize populations male emergence peaked in mid-July (14–19 July) and gradually tapered off, leading to a significant time effect in repeated measures (table 4). Effects of maize line had a consistent impact on male emergence and male weight throughout the season for both test groups (table 4).

When assessing the experimental synthetic maize populations and using root fresh weight as a covariate, maize line did not have a significant impact on the number of males (P = 1.0), but did significantly impact male weight (P = 0.04; table 5). Significantly heavier males emerged from CRW3(C6) roots than from BS29-18-01 (P = 0.05) and BS29-07-01 roots (P = 0.05; table 5).

Maize line had a significant impact on the number and weight of males emerging from maize hybrids when root fresh weight was used as a covariate ($d.f._{3,11}$, P = 0.002; $d.f._{3,11}$, P = 0.009). Significantly fewer males emerged from the transgenic DeKalb® 46-23 hybrid compared with the other maize hybrids (P < 0.007; table 6). In addition, males from the transgenic DeKalb® 46-23 hybrid were significantly lighter than those from DeKalb® 46-26 (P < 0.006) and the highly susceptible hybrid (B37 × H84, P = 0.04; table 6).

For maize hybrids, emergence data (number of adult females and female weight) from 7 August and 16 August were excluded from repeated measures analysis

Table 4. *Statistical information for 2006 rootworm emergence data*

	Number of males	Male dry weight	Number of females	Female dry weight
SP lines[1]				
Time				
Wilks λ	0.624	0.676	0.782	0.768
d.f.	5,22	5,22	8,19	8,19
F	2.648	2.105	0.664	0.717
P	0.051	0.103	0.717	0.674
Time × line				
Wilks λ	0.145	0.158	0.075	0.019
d.f.	40,98	40,98	64,116	64,116
F	1.373	1.299	1.032	1.800
P	0.105	0.150	0.435	0.003
Time × covariate				
Wilks λ	0.618	0.661	0.789	0.807
d.f.	5,22	5,22	8,19	8,19
F	2.72	2.261	0.634	0.568
P	0.046	0.084	0.740	0.791
Hybrids				
Time				
Wilks λ	0.875	0.870	0.707	0.605
d.f.	2,10	2,10	6,6	6,6
F	0.712	0.748	0.415	0.653
P	0.512	0.498	0.845	0.691
Time × line				
Wilks λ	0.755	0.864	0.123	0.057
d.f.	6,20	6,20	18,17	18,17
F	0.502	0.253	1.065	1.700
P	0.800	0.952	0.449	0.138
Time × covariate				
Wilks λ	0.864	0.869	0.706	0.560
d.f.	2,10	2,10	6,6	6,6
F	0.789	0.752	0.417	0.786
P	0.481	0.496	0.845	0.612

[1]SP, experimental synthetic maize populations.

Table 5. *Mean numbers of emerged rootworm adults and average dry weight (mg) per adult for nine experimental synthetic maize populations grown in field trials near Brookings, SD during 2006*

Maize line	Number of males	Male dry weight	Number of females	Female dry weight[1]
NGSDCRW1 (S2)C4	5.3 ± 2.4 a	3.7 ± 0.8 ab	18.8 ± 5.8 a	8.5 ± 1.4
CRW8-1	9.8 ± 3.8 a	4.3 ± 0.7 ab	30.3 ± 10.3 a	10.5 ± 1.1
CRW8-2	3.3 ± 2.0 a	3.1 ± 1.3 ab	19.0 ± 10.5 a	8.6 ± 2.6
CRW8-3	2.8 ± 1.4 a	2.2 ± 0.8 ab	17.5 ± 5.9 a	9.1 ± 2.7
CRW2(C5)	1.5 ± 0.5 a	2.2 ± 0.9 ab	11.0 ± 2.5 a	6.7 ± 1.2
CRW3(C6)	4.8 ± 1.6 a	5.1 ± 1.1 a	19.5 ± 8.9 a	5.1 ± 1.8
BS29-18-01	0.8 ± 0.5 a	0.6 ± 0.4 b	5.3 ± 4.0 a	3.8 ± 1.9
BS29-07-01	0.3 ± 0.3 a	0.5 ± 0.5 b	6.3 ± 4.5 a	5.3 ± 3.2
BS29-11-01	4.3 ± 3.3 a	2.3 ± 1.4 ab	23.8 ± 17.8 a	6.9 ± 3.1

Within each column means ± SEM followed by the same letter are not significantly different (P > 0.05) from an ANOVA analysis with log fresh root weight as a covariate.
[1]Significance not reported because of a significant time × line interaction in repeated measures ANOVA.

Maize line[1]	Number of males	Male dry weight	Number of females	Female dry weight
DeKalb® 46-23 CRW	0 ± 0 a	0 ± 0 a	1.5 ± 1.5 a	1.3 ± 1.3 a
DeKalb® 46-26	2.0 ± 0.9 b	3.6 ± 1.6 b	7.0 ± 4.7 a	3.2 ± 1.9 ab
B73 × MO17	2.0 ± 0.6 b	2.4 ± 0.6 ab	11.8 ± 2.5 a	9.7 ± 2.1 b
B37 × H84	1.3 ± 0.3 b	1.9 ± 0.1 b	7.8 ± 3.5 a	3.8 ± 1.0 ab

Within each column means ± SEM followed by the same letter are not significantly different (P > 0.05) from an ANOVA analysis with log fresh root weight as a covariate.
[1]DeKalb® 46-23 CRW is a transgenic resistant hybrid, DeKalb®46-26 is the isoline of DeKalb® 46-23 CRW, B73 × MO17 is susceptible, and B37 × H84 is highly susceptible.

Table 6. *Mean numbers of emerged rootworm adults and average dry weight (mg) per adult for four maize hybrids grown in field trials near Brookings, SD during 2006*

because all values were zeros, whereas data from all dates were used for experimental synthetic maize populations. In both experimental synthetic maize populations and maize hybrids, female emergence peaked in mid- to late-July (19–24 July) and gradually tapered off, although there were no significant time effects in repeated measures for number of females or female weight (table 4). Maize line had a consistent impact on female emergence throughout the season for both test groups (table 4). When root fresh weight was used as a covariate, maize line did not have a significant impact on the number of females that emerged from the experimental synthetic maize populations (P = 0.41; table 5). However, for synthetic maize populations, maize line had an inconsistent impact on average dry female weight throughout the sampling period (table 4), and thus profile analysis was used to explore each sampling date. Maize line had a significant impact on female weight on 14 and 28 July (table 4), which was likely driven by the high mean weight of adult females from CRW8-1 compared with the low mean weight of females from BS29-18-01, although P-values from a Tukey's HSD test between the two lines were only marginally significant on 14 July (P = 0.08) and not significant on 28 July (P = 0.55).

Although the mean number of females that emerged from the transgenic DeKalb® 46-23 hybrid was much lower than the other maize hybrids, maize line only had a marginal effect on female density when root fresh weight was used as a covariate ($d.f._{3,11}$, P = 0.08; table 6). Maize line did significantly impact female weight ($d.f._{3,11}$, P = 0.02), with lighter females emerging from the transgenic DeKalb® 46-23 hybrid compared with the susceptible B73 × MO17 hybrid (P = 0.01; table 6).

When evaluating both experimental synthetic maize populations and maize hybrids, male density was positively correlated with male weight (P < 0.001, R^2 = 0.82), and female density was positively correlated with female weight (P < 0.001, R^2 = 0.75; fig. 1). The total dry weight of males that emerged from BS29-07-01, a line with low emergence, was 0.2 mg (number of males × male dry weight; table 5). In contrast, the total dry weight of males from CRW3(C6), a line with high emergence, was 24.5 mg (table 5). For these two maize lines, this difference in male weight is a multiple of approximately 120.

4 Discussion

Because plants have a multifaceted response to herbivorous pests, maize germplasm that is potentially resistant to corn rootworms must be evaluated in several ways, including assessing whether each line exhibits resistance (non-preference and antibiosis), tolerance, or both. We selected experimental lines with a gradient of rootworm resistance levels and expected to observe a broad range of root damage ratings. However, ratings were lower than anticipated, with the majority of lines having root damage ratings of < 4.0 in both years.

Among the four maize hybrids, the transgenic resistant hybrid (DeKalb® 46-23) had significantly lower root damage ratings and male rootworm emergence compared with the other maize hybrids, although the transgenic resistant hybrid did not produce new root growth, because there was little or no feeding damage. Its isoline (DeKalb® 46-26) had the second lowest mean root damage rating, and it is likely that the performance of the DeKalb® hybrids was influenced by their seed treatments, which included the neonicotinoid insecticide clothianidin. Clothianidin acts as an antifeedant, and is effective against corn rootworms (Andersch and Schwarz 2003). The

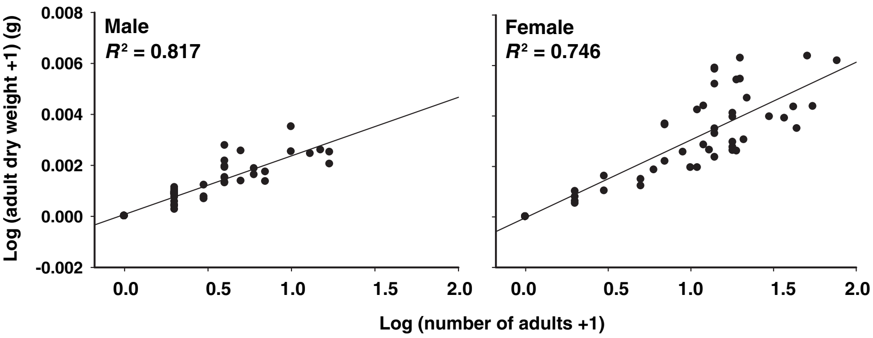

Fig. 1. *Linear regression between number of adult male and female western corn rootworms that emerged from 13 maize lines and dry weight per male (left) and female (right) grown in field trials near Brookings, SD in 2005 and 2006. Values are log (X + 1) transformed*

susceptible hybrid B73 × MO17 had the third highest mean root damage rating, while the highly susceptible hybrid B37 × H84 had the highest mean root damage rating.

Among the experimental synthetic maize populations, CRW8-3 had the lowest mean root damage rating, which was comparable with that of the non-transgenic hybrid DeKalb® 46-26, and appeared to be tolerant to western corn rootworms, as evidenced by high mean root fresh weight and compensatory root growth ratings. NGSDCRW1(S2)C4, a maize line with rootworm resistance based on high root-pull measurements (Kahler et al. 1985) had significantly heavier roots than the other synthetic maize populations. Although maize lines that are tolerant to rootworm damage (as indicated by heavy root systems and high compensatory root growth ratings) may have reduced root damage, this does not necessarily translate into increased yield (Gray and Steffey 1998), and maize lines with inherently small root systems may have similar yields to those with large root systems.

BS29-11-01 was the most susceptible synthetic maize population, and had a mean root damage rating that was greater than the highly susceptible maize hybrid B37 × H84. This line also had the lowest mean root fresh weight and one of the lowest mean compensatory root growth ratings, and did not appear to have any rootworm resistance. BS29-07-01 performed very similar to BS29-11-01 in terms of root damage and root fresh weight; however, male rootworms that emerged from BS29-07-01 weighed significantly less, which may indicate that this maize line is not a high quality resource for rootworm development (Moeser and Vidal 2004) or that there was density-dependent rootworm mortality (Moeser and Hibbard 2004). BS29-18-01 also had low mean male emergence and weight. However, the mean root damage rating for this maize line was not statistically different from the synthetic maize population with the lowest mean root damage rating, which may indicate some degree of antibiosis or non-preference, although nutritional quality and density-dependent mortality may also be factors.

Both female and male size influences eggs production in northern corn rootworms (*Diabrotica barberi* Smith and Lawrence), with larger females laying more eggs and the larger the male partner the more eggs produced (Bryan W. French, personal communication). Thus, maize line characteristics that influence adult emergence could have a major impact on rootworm populations in subsequent years within agroecosystems, and utilizing maize lines with low adult emergence could enhance areawide rootworm population management programmes, especially when combined with adulticides.

Based on these evaluations, there is potential to improve maize resistance to the western corn rootworm by combining the traits for reduced root damage derived from CRW8-3, traits for low adult emergence from BS29-18-01, and traits for high root weight from NGSDCRW1(S2)C4, although yield parameters for these lines need to be evaluated. Maize lines with multiple beneficial traits could be an important component of an integrated pest management package, that could also utilize transgenic resistant hybrids, hybrids with non-transgenic resistance, crop rotation and insecticidal seed treatments.

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